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Molecular phylogeny of large miliolid foraminifera (Soritacea Ehrenberg 1839)

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Abstract

The foraminiferal superfamily Soritacea belongs to the suborder Miliolina and is divided in two families, Peneroplidae and Soritidae, the latter one comprising two subfamilies, Archaiasinae and Soritinae. Phylogenetic relationships of 11 genera of soritid foraminifera were investigated by sequencing the complete SSU rDNA gene for 25 specimens. Additionally, partial SSU rDNA sequences were obtained from another 15 specimens of Soritinae. DNA sequence analysis confirms the monophyly of each family. Caribbean Archaiasinae form a monophyletic clade with Pacific Laevipeneroplis at the base. The genus Parasorites apppears as a sister taxa to Soritinae. Complex morphological features that characterize the genus Marginopora seem to have evolved independently at least twice, as the examined representatives cluster within two other soritine genera. Molecular analysis further shows that *Sorites orbiculus* and *Sorites marginalis* represent two different morphotypes of one species. Our data indicate that morphological changes and acquisition of new endosymbiont types in each group played an important role in the adaptation and radiation of Soritacea.

Keywords: molecular phylogeny; foraminifera; soritacea; SSU rDNA

1. Introduction

Large symbiont-bearing foraminifera of the superfamily Soritacea inhabit recent tropical and subtropical shallow water seas. They are also common fossils in Mesozoic and Cenozoic neritic sediments and are used in micropaleontology for stratigraphical and environmental analyses, to establish biozonations (Hottinger, 1983; Cahuzac, Poignant, 1997). Their evolutionary history, characterized by rapid radiations and adaptations is relatively well known and has been the subject of several extensive studies (e.g. Lehmann, 1961; Seiglie et al., 1976; Lee and Hallock, 1987; Gudmundsson, 1994).

The superfamily Soritacea comprises two extant families, Peneroplidae and Soritidae, the latter one being subdivided into Archaiasinae and Soritinae (Gudmundsson, 1994). Peneroplid tests are characterized by planispiral growth, and red to purple color can be seen through the porcellaneous shell in living individuals, a fact that derives from their rhodophycean endosymbionts (Lee, 1990). Archaiasinae show an arciform growth mode and grass green to olive color when alive, due to their chlorophycean endosymbionts. Soritinae exhibit flabelliform growth stages and generally harbour dinoflagellates as symbionts, resulting in a brownish color in living representatives

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Table 1
Collection localities and sequenced regions of the SSU rRNA gene for Alveolinidae and Soritacea. Note: Letters a-l indicate different specimens. + = complete SSu rDNA sequences. * = partial SSU rDNA sequences.

Species	Locality	Collection date	SSU rDNA data	Accession numbers
Alveolinidae				
Alveolinella quoyi	Sesoko, Japan	Oct-96	+	AJ404294
Borelis schlumbergeri	Bermuda	May-96	+	AJ404295
Soritacea				
Dendritina zhengae	Sesoko, Japan	Nov-96	+	AJ404297
Peneroplis planatus	Lizard Island, Australia	Aug-97	+	AJ404296
Peneroplis pertusus	St. Cyr, France	Apr-95	+	Z69604
Cyclorbiculina compressa	Florida Keys, Conch Reef	Jul-98	+	AJ404303
Broeckina sp.	Florida Keys, Conch Reef	Jul-98	+	AJ404304
Archaias angulatus	Florida Keys, Keys Marine Laboratory	Jul-98	+	AJ404302
Androsina lucasi	Florida Keys, Sugarloaf Key	Jul-98	+	AJ404301
Laevipeneroplis proteus	Florida Keys, Tennessee Reef	Jul-98	+	AJ404299
Laevipeneroplis bradyi	Florida Keys, Conch Reef	Jul-98	+	AJ404298
Laevipeneroplis sp.	Guam, Gun Beach	Mar-00	+	AJ404300
Parasorites sp. a	Guam, Piti	Jul-99	+	AJ404305
Parasorites sp. b	Lizard Island, Australia	Aug-97	+	AJ404306
Parasorites sp. c	Sesoko, Japan	Oct-96	+	AJ404307
Sorites orbiculus a	Safaga, Egypt	Jun-96	+	AJ132369
Sorites orbiculus b	Lizard Island, Australia	Aug-97	+	AJ404309
Sorites orbiculus c	Florida Keys, Tennessee Reef	Jul-98	*	AJ278056
Sorites marginalis d	Florida Keys, Conch Reef	Jul-98	+	AJ404308
Sorites sp. E	Elat, Israel	Apr-99	*	AJ278057
Sorites orbiculus f	Taba, Israel	Apr-99	+	AJ404310
Sorites sp. g	Elat, Israel	Apr-99	+	AJ404311
Sorites orbiculus h	Guam, Double Reef	Jul-99	*	AJ278054
Sorites orbiculus i	Guam, Piti	Jul-99	*	AJ278053
Sorites orbiculus j	Guam, Harbour	Jul-99	*	AJ278055
Sorites sp. k	Elat, Israel	Apr-99	*	AJ278052
Sorites sp. l	Elat, Israel	Apr-99	+	AJ404313
Marginopora vertebralis a	Lizard Island, Australia	Aug-97	*	AJ278060
Marginopora vertebralis b	Lizard Island, Australia	Aug-97	+	AJ404312
Marginopora vertebralis c	Lizard Island, Australia	Aug-97	*	AJ278058
Marginopora vertebralis d	Guam, Double Reef	Jul-99	*	AJ278059
Marginopora vertebralis e	Guam, Luminao Beach	Jul-99	*	AJ278061
Marginopora vertebralis f	Guam, Pago Bay	Jul-99	*	AJ278062
Amphisorus hemprichii a	Sesoko, Japan	Jun-98	+	AJ404314
Amphisorus hemprichii b	Elat, Israel	Apr-99	+	AJ404315
Amphisorus hemprichii c	Taba, Israel	Apr-99	*	AJ278049
Amphisorus hemprichii d	Elat, Israel	Apr-99	*	AJ278048
Marginopora cf. kudakajimaensis a	Sesoko, Japan	Dec-96	*	AJ278051
Marginopora cf. kudakajimaensis b	Guam, Double Reef	Jul-99	+	AJ404316
Marginopora cf. kudakajimaensis c	Guam, Double Reef	Jul-99	*	AJ278050

Table 2
Taxonomic Appendix

Alveolinella quoyi d'Orbigny = *Alveolina quoii* (d'Orbigny, 1826)
Borelis schlumbergeri Reichel = *Neoalveolina pygmea* (Hanzawa) *schlumbergeri* (Reichel, 1937)
Dendritina zhengae Ujiie in Hatta and Ujiie, 1992
Peneroplis planatus Fichtel and Moll = *Nautilus planatus* (Fichtel and Moll, 1798)
Peneroplis pertusus Forskal = *Nautilus pertusus* (Forskal, 1775)
Cyclorbiculina compressa d'Orbigny = *Orbiculina compressa* (d'Orbigny, 1839)
Archaias angulatus Fichtel and Moll = *Nautilus angulatus* (Fichtel and Moll, 1798)
Androsina lucasi Lévy, 1977
Laevipeneroplis proteus d'Orbigny = *Peneroplis protea* (d'Orbigny, 1839)
Laevipeneroplis bradyi Cushman = *Peneroplis bradyi* (Cushman, 1930)
Sorites orbiculus Forskal = *Nautilus orbiculus* (Forskal, 1775)
Sorites marginalis Lamarck = *Orbulites marginalis* (Lamarck, 1816)
Marginopora vertebralis Quoi and Gaimard in Blainville, 1830
Amphisorus hemprichii Ehrenberg 1839
Marginopora kudakajimaensis Gudmundsson 1994

(McEnery and Lee, 1981; Lee and Hallock, 1987; Gudmundsson, 1994).

The systematics of Soritacea is based on morphological characters of their tests, e.g. growth form, endoskeletal and exoskeletal features (Hofker, 1950, 1951, 1952; Loeblich and Tappan, 1964). Carpenter (1861) considered the Peneroplidae and Soritidae to be monophyletic groups with a common ancestor. Brady (1884) believed Peneroplidae, Archaiasinae and Soritinae to be related and to stem from a common ancestor. Hofker (1953) placed Cretaceous *Praepeneroplis* at the origin of Soritacea and considered peneroplid and archaiasine forms to be more basal than soritines. Gudmundsson (1994) put peneroplids at the base of his cladogram, followed by archaiasines, with soritines at the top position.

Whereas the taxonomic status of the different families is well established, the classification is less resolved for some of the genera, depending on which morphological characters are regarded as important for their distinction and on the interpretation of these characters (advanced or ancestral state, homologous vs. non-homologous features; for a review see Gudmundsson, 1994).

Molecular data offer the advantage that they are independent of morphological characters and permit the consideration of controversial taxonomic issues from a different perspective. We report here the first complete sequences of small subunit ribosomal RNA genes (SSU rDNA) of eleven genera of Soritacea and two genera of Alveolinidae, another group of large miliolids. We compare and discuss molecular and morphological data sets, which both confirm the distinction of the families and subfamilies, while showing contradictory results for some of the investigated genera.

Plate I (p. 60).
1. *Sorites orbiculus* f, Taba, side view showing sutures.
2. *Sorites orbiculus* f, Taba, apertural view.
3. *Amphisorus hemprichii*, Sesoko, side view showing sutures. No sequence is available for this specimen.
4. *Amphisorus hemprichii*, Sesoko, same specimen, apertural view.
5. *Sorites* sp. l, Elat, side view showing sutures.
6. *Sorites* sp. l, Elat, apertural view.

Plate II (p. 61).
1. *Parasorites* sp. a, Guam, Piti, side view showing sutures.
2. *Parasorites* sp. a, Guam, Piti, apertural view.
3. *Marginopora vertebralis* d, Guam, Double Reef, side view showing sutures.
4. *Marginopora vertebralis* d, Guam, Double Reef, apertural view.
5. *Marginopora* cf. *kudakajimaensis* c, Guam, Double Reef, side view showing sutures.
6. *Marginopora* cf. *kudakajimaensis* c, Guam, Double Reef, apertural view.

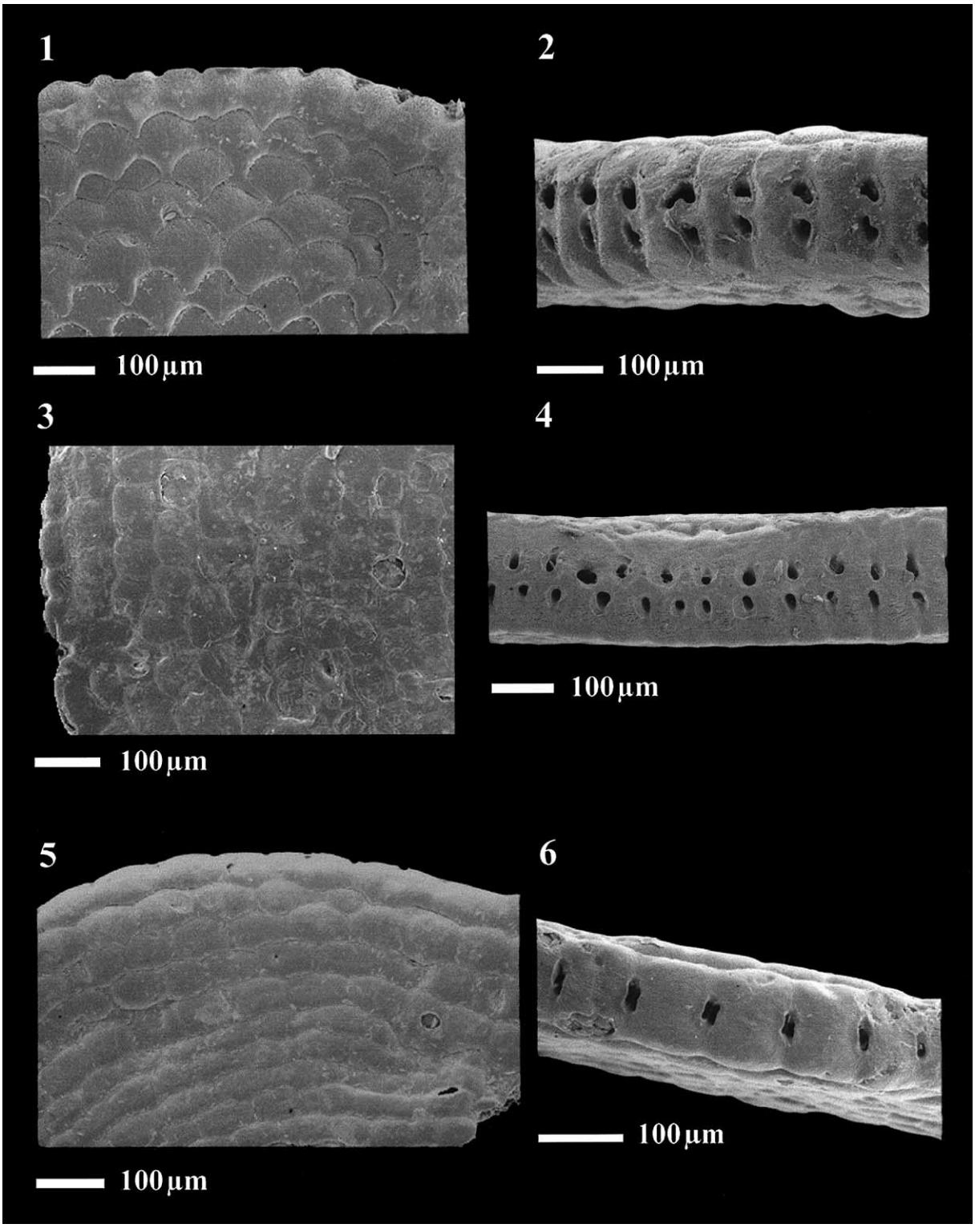

Plate I (for description see p. 59).

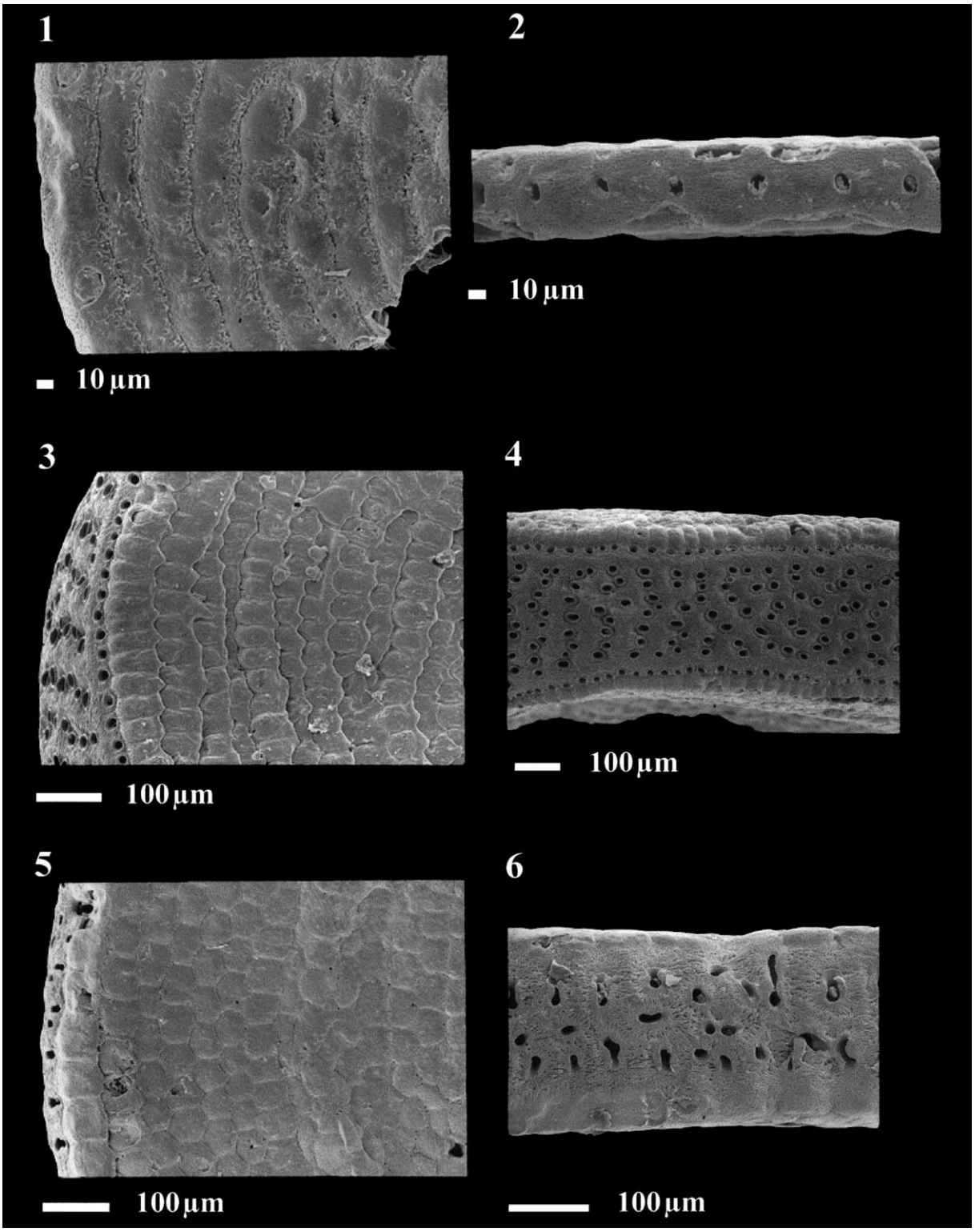

Plate II (for description see p. 59).

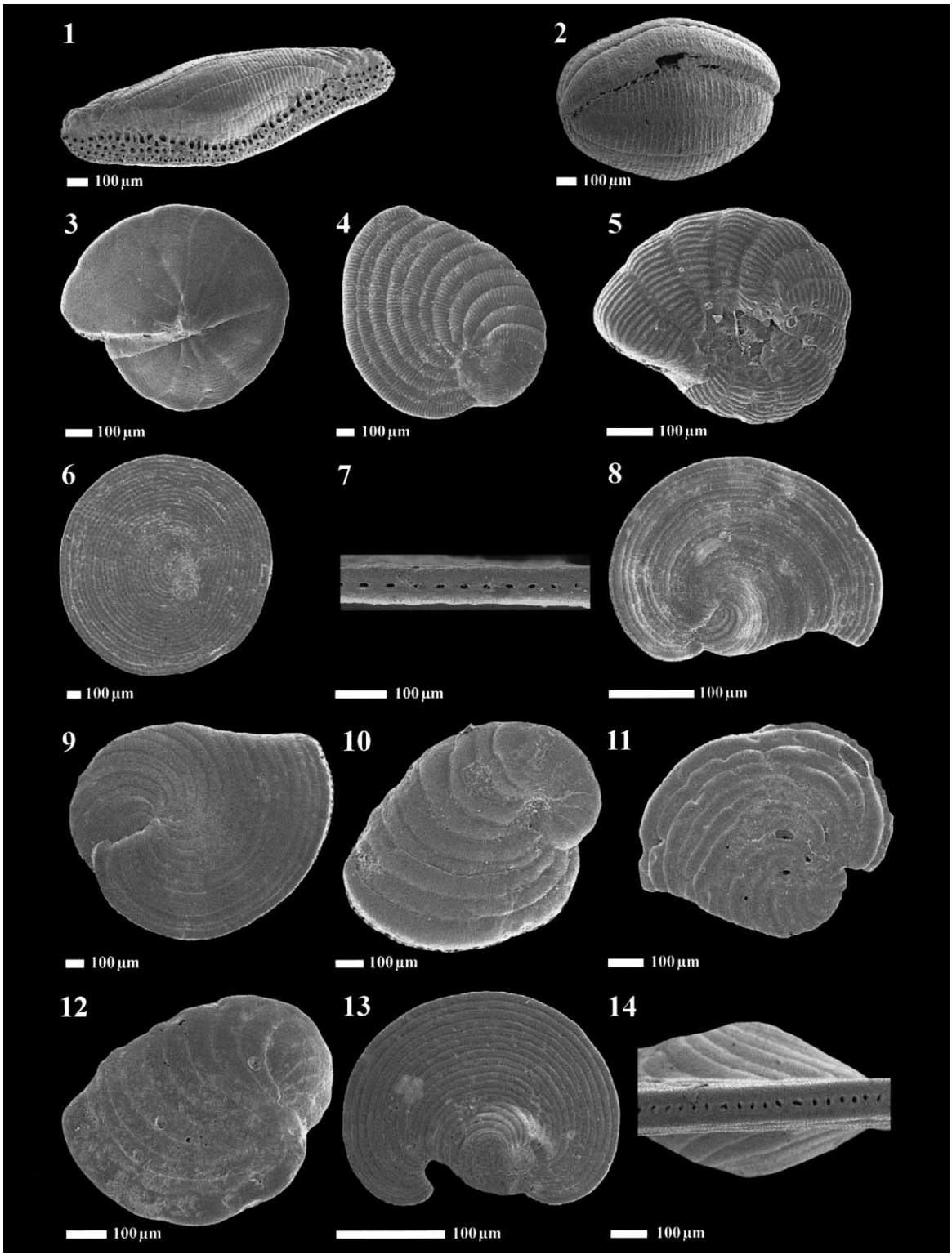
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Plate III.

Table 3
List of amplification and sequencing primers for the SSU r RNA gene in Alveolinidae and Soritacea. Note: EMBL/GenBank accession numbers of sequences used as references for primer positions: K-01593 (rat), AJ-132374 (reticulomyxa).

Primer	Sequence	Orientation	Specifity	Position in *Rattus norvegicus*	Position in *Reticulomyxa filosa*
sA10	ctcaaagattaagccatgcaagtgg	Forward	Foraminiferal	35–59	1–25
s13	gcaacaatgattgtataggc	Reverse	Foraminiferal	647–666	1131–1150
s6r	gggcaagtctggtgc	Forward	Broad	603–617	1087–1101
s17	cggtcacgttcgttgc	Reverse	Foraminiferal	1380–1395	2658–2673
s14F3	acgca(ac)gtgtgaaacttg	Forward	Foraminiferal	1181–1198	2277–2294
SBF	gtaggtgaacctgc(tc)gatggatca	Reverse	Foraminiferal	1848–1871	3336–3348

2. Material and methods

2.1. Cell collection

The living representatives of Soritacea and Alveolinidae used in the present study were collected from the western Pacific, the Red Sea and the western North Atlantic (Table 1). Representatives of all recent soritacean genera were investigated in the present work, with the exception of three peneroplid genera (*Coscinospira*, *Monalysidium*, *Spirolina*) for which no living representatives were available. A taxonomic appendix of the investigated species is given in Table 2.

Individuals were collected either by SCUBA diving, snorkling, or by taking surface sediment samples, macrophytic algae and sea grass (*Thalassia testudinum*) by hand. Living specimens showing extended pseudopodia were identified by the use of a stereomicroscope and isolated for subsequent studies. Some representatives of every investigated species were examined with the scanning electron microscope (SEM) and selected photographs are presented in Plates I–III.

2.2. DNA extraction, amplification, cloning and sequencing

Before extracting DNA, each specimen was transferred into an individual receptacle containing filtered seawater and cleaned by brushing. A total of 42 DNA extractions were used in the present study. For some of the larger living soritine specimens, DNA was extracted from half of the test while the other half was kept for morphological investigations with the SEM. DNA of some specimens was extracted by grounding each individual separately in DOC extraction buffer, following incubation for 1 h at 60°C and short centrifugation to remove insoluble material (Holzmann and Pawlowski, 1996). DNA extraction of the remaining specimens was performed by using DNeasy Plant Mini Kit (Qiagen).

SSU rDNA was amplified by PCR in a total volume

Plate III. (No sequences are available for the foraminiferal specimens in this Plate)
1. *Alveolinella quoyi*, Sesoko, external view showing apertures.
2. *Borelis schlumbergeri*, Elat, external view showing apertures.
3. *Dendritina zhenghae*, Sesoko, external view.
4. *Peneroplis planatus*, Lizard Island, external view.
5. *Peneroplis pertusus*, Florida Keys, Conch Reef, external view.
6. *Broeckina* sp., Florida Keys, Conch Reef, external view.
7. *Broeckina* sp., Florida Keys, Conch Reef, same specimen, apertural view.
8. *Cyclorbiculina compressa*, Florida Keys, Conch Reef, external view.
9. *Archaias angulatus*, Florida Keys, Keys Marine Laboratory, external view.
10. *Androsina lucasi*, Florida Keys, Sugarloaf Key, external view.
11. *Laevipeneroplis proteus*, Florida Keys, Tennessee Reef, external view.
12. *Laevipeneroplis bradyi*, Florida Keys, Conch Reef, external view.
13. *Laevipeneroplis* sp., Guam, Gun Beach, external view.
14. *Laevipeneroplis* sp., Guam, Gun Beach, same specimen, apertural view, showing single row of apertures.

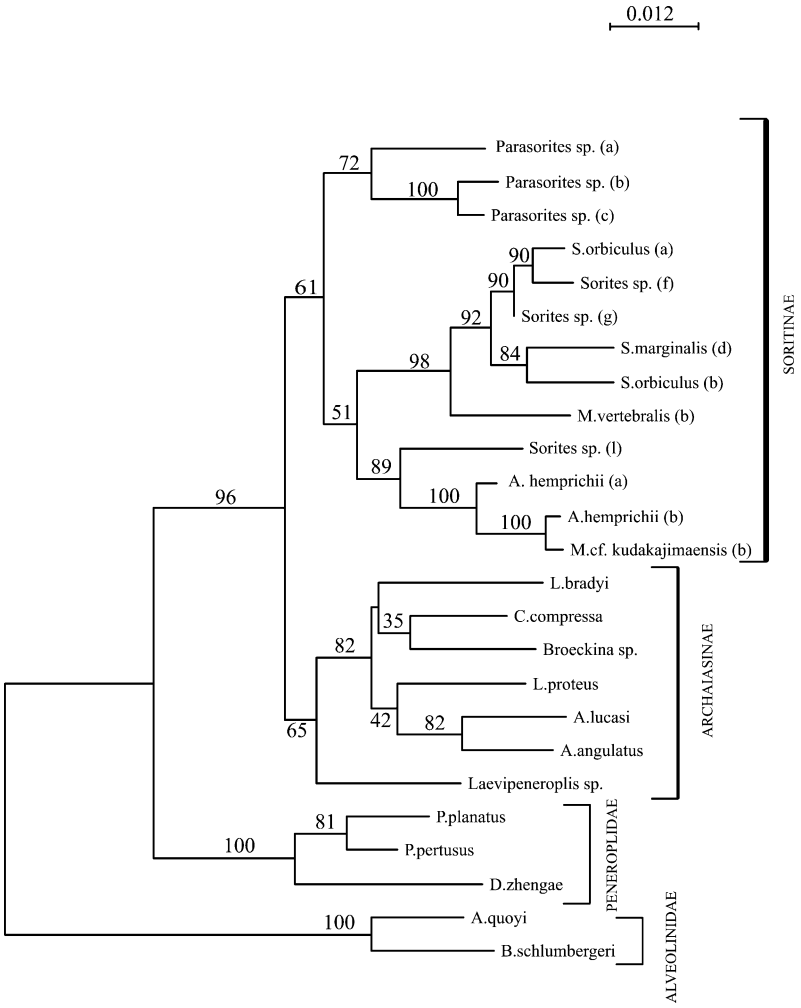

Fig. 1. Phylogenetic tree based on the complete SSU rRNA gene of two alveolinid genera and eleven soritacean genera using maximum likelihood analysis. The tree is rooted in Alveolinidae. Bootstrap values are based on 100 resampling. 1664 out of a total of 3006 sites were used for analysis.

of 50 μl. The thermal cycle parameters consisted of 40 cycles of 30 s at 94°C, 30 s at 50°C and 120 s at 72°C, followed by 5 min at 72°C for final extension. The amplified PCR products were purified using High Pure PCR Purification Kit (Roche Diagnostics), then ligated into pGEM-T Vector system (Promega) and cloned in XL-2 Ultracompetent Cells (Stratagene). Sequencing reactions were prepared by using ABI-PRISM Big Dye Terminator Cycle Sequencing Kit and analyzed with an ABI-377 DNA sequencer (Perkin–Elmer), all according to the manufacturer's instructions.

The complete SSU rDNA was amplified in three overlapping fragments by using the following primer pairs: sA10–s13, s6r–s17, s14F3–sBf (Table 3). Partial SSU rDNA sequences were obtained by amplification with the primer pair s14F3–sBf (Table 3). The new sequences reported in this paper have been deposited in the EMBL/GenBank database under accession numbers AJ278048-AJ278062 and AJ404294-AJ278062 (Table 1). The sequences of *P. pertusus* (Z69604) and *Sorites orbiculus* (AJ132369) were published by Pawlowski et al. (1999).

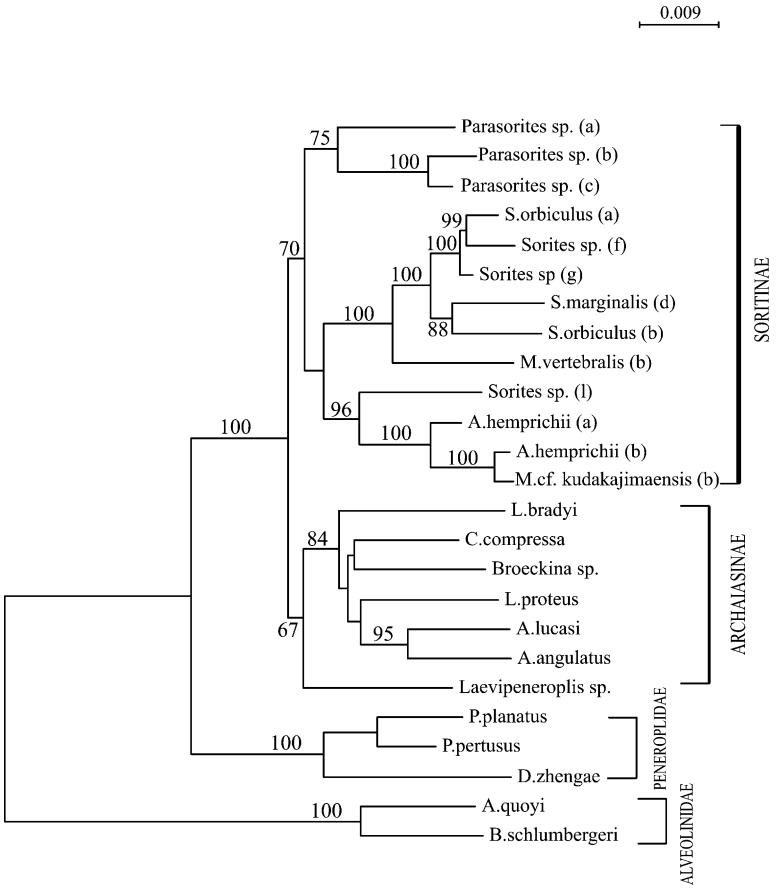

Fig. 2. Phylogenetic tree based on the complete SSU rRNA gene of two alveolinid genera and eleven soritacean genera using neighbor joining analysis. The tree is rooted in Alveolinidae. Bootstrap values are based on 1000 resampling.1664 out of a total of 3006 sites were used for analysis.

2.3. Sequence analysis

Sequences were aligned manually by using the GDE 2.2 software (Larsen et al., 1993). Selected sites in homologous regions without gap were retained for phylogenetic analyses. Analyses are based on the following methods: the neighbor–joining (NJ) method (Saitou and Nei, 1987), applied to distances corrected for multiple hits and for unequal transition and transversion rates, using Kimura's two-parameter model (Kimura 1980); the maximum likelihood (ML) method as implemented in the fast DNAm1 program (Olsen et al., 1994); and the maximum parsimony (MP) method, using PAUP* 4.0b version (Swofford, 2000). NJ analysis of the complete SSU rDNA gene was additionally tested by using the LogDet model (Lockhart et al., 1994), because of the biased base composition in Miliolida (G + C content of about 30%), which yielded the same results as with Kimura's two-parameter model. Parsimony analysis consisted of heuristic searches with 100 random-addition replicates using tree bisection–reconnection (TBR) branch swapping and stepwise addition of taxa. The reliability of internal branches was assessed by bootstrapping (Felsenstein, 1988) with 1000 resampling for the NJ and 100 resampling for the ML and MP trees, respectively. The PHYLO_WIN program (Galtier and Gouy, 1996) was used for distance computations, NJ and ML tree-building and bootstrapping.

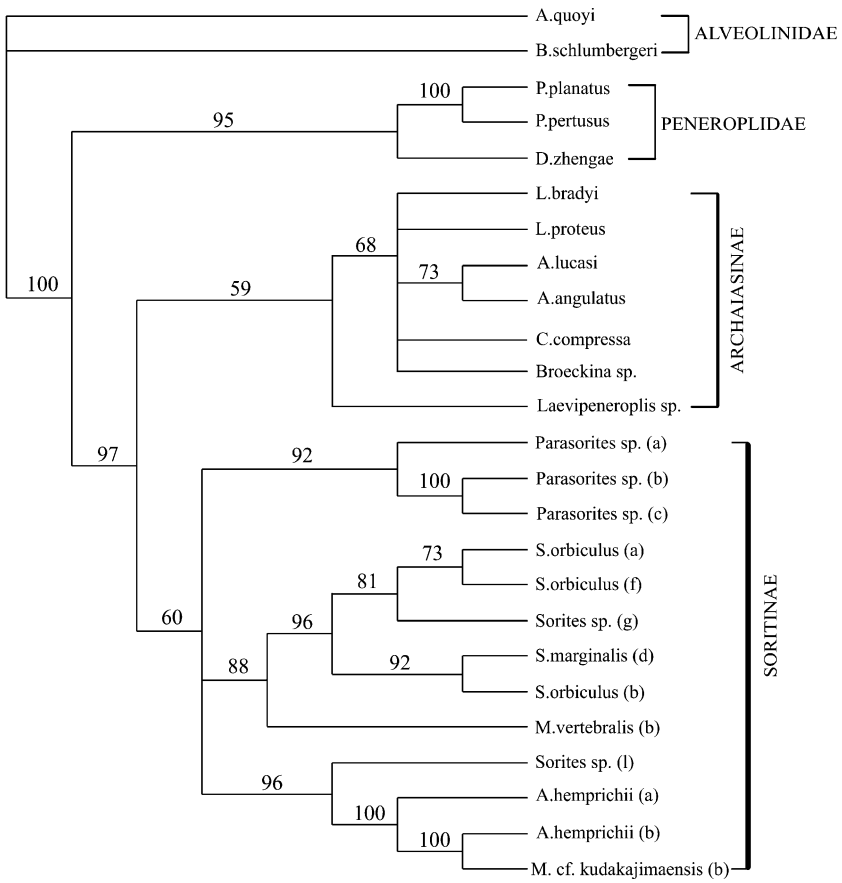

Fig. 3. Phylogenetic tree based on the complete SSU rRNA gene of two alveolinid genera and eleven soritacean genera using maximum parsimony analysis. 814 out of 3006 sites are parsimony-informative. The total length of the most parsimonous tree is 2719, which equals the length of the best tree overall. Ci and ri indices are 0.5355 and 0.5069, respectively. The tree is rooted in Alveolinidae. Bootstrap values are based on 100 resampling.

3. Results

3.1. Sequence data

The complete SSU rRNA gene was sequenced for 23 specimens of Soritacea and 2 specimen Alveolinidae (Table 1). The length of the sequences ranges from 2126 to 2744 basepairs (BP), which is about one and a half as much as in other eukaryotes. This unusual length results from several insertions in conserved regions of the gene that are unique to foraminifera. The sequences of Soritacea and Alveolinidae, however, are relatively short compared to other foraminiferal species, where the length of the SSU rDNA easily exceeds 3000 BP (Pawlowski, 2000). The G + C content is low and ranges from 27.5 to 30.6%. Miliolida in general are among those foraminiferal groups with the lowest G + C content (~30%), a fact that is due to long series of A + T in expansion segments.

For 15 specimens of Soritinae, partial SSU rDNA sequences were obtained (Table 1). The sequences contain between 814 and 1018 BP, their G + C content ranges from 28.9 to 31.8%. They correspond to the 3′ terminal region of *Rattus norvegicus* (K-01593) starting at the position 1181 and ending at position 1871 (Table 3). The examined fragment includes six variable regions, among them, region I corresponds to the universal variable region V6 of the prokaryotic secondary structure model (Neefs et al., 1993).

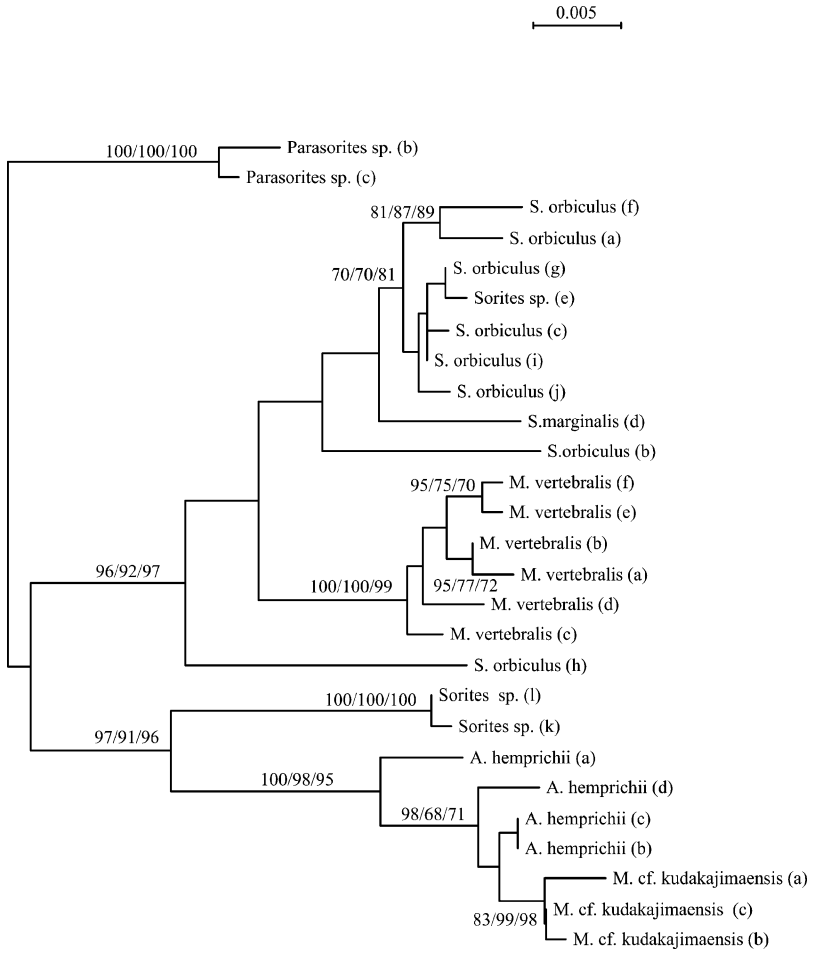

Fig. 4. Phylogenetic tree based on partial SSU r DNA sequences of 27 soritine specimens using neighbor joining method. Bootstrap values are based on 1000 resampling for the NJ tree and on 100 resampling for the ML and the MP tree (first, second and third numbers, respectively). Total length of the most parsimonous tree is 287. The partial SSU rDNA alignment consists of 1095 sites, among them, 778 were used for NJ and ML analysis and 122 are parsimony informative. Ci and ri indices are 0.7038 and 0.8741, respectively.

3.2. Phylogenetic analysis

Analysis of the complete SSU rRNA gene conducted by ML, NJ and MP methods results in phylogenetic trees that are largely congruent. Alveolinidae were chosen as an outgroup because they represent the most closest sister group to Soritacea among all investigated miliolid Foraminifera. Fig. 1 represents the ML tree with Soritacea forming two very well supported (100% and 96% bootstrap) monophyletic clusters corresponding to the families Peneroplidae and Soritidae (sensu Gudmundsson, 1994). Soritidae are divided in two subgroups that coincide with the subfamilies Archaiasinae and Soritinae (sensu Gudmundsson, 1994), the latter one also including the genus *Parasorites*. Although relationships within the Soritidae are not well established, as the bootstrap support for each subfamily is lower than 70% (Hillis and Bull, 1993), the composition of both subfamilies remains stable regardless of the applied algorithm. The only differences between the ML tree shown in Fig. 1, and the NJ and MP trees (Figs. 2 and 3, respectively) are changes in the branching position of some species. Compared to the ML tree, *Laevipeneroplis bradyi* clusters between *Laevipeneroplis* sp. and the remaining archaiasine species

in the NJ tree (Fig. 2). Branching positions within the Archaiasinae change in the MP tree (Fig. 3): *Laevipeneroplis* sp. keeps its basal position and *Archaias angulatus* and *Androsina lucasi* form a group (bootstrap value of 73%), but the phylogenetic relationships between the remaining archaiasine species are not resolved. Furthermore, *Parasorites* does not appear at the base of the Soritinae, but builds a sister group to the *Amphisorus/Marginopora kudakajimaensis* and *Sorites/Marginopora vertebralis* clade (bootstrap value of 60%).

To improve the resolution of the relationships within the Soritinae, 15 additional partial SSU rDNA sequences of Soritinae have been obtained. The examined fragment prooves to be well suited to investigate intrageneric relationships in Foraminifera (De Vargas et al., 1999; Pawlowski, 2000). Additional informative sites were gained by excluding more distantly related groups of Soritacea from the analysis. A total of 27 sequences, including *Parasorites* as an outgroup has been analysed by using NJ method (Fig. 4). The result confirms the division of Soritinae in two distinctive clades as it was already suggested by the analysis of complete SSU rDNA sequences. One clade is composed of *Amphisorus hemprichii* and *Marginopora* cf. *kudakajimaensis*, as well as two specimens of *Sorites* (*Sorites* sp_k and *Sorites* sp._l). The second clade comprises the remaining *Sorites* specimens (specimens a–j) and *Marginopora vertebralis*, the latter one forming a monophyletic group, supported by 99–100% bootstrap value (Fig. 4). One sequence of *Sorites* (*Sorites orbiculus*_h) branches at the base of the *Sorites/Marginopora* clade. Analyses with ML and MP method (trees not shown) yield congruent results. Changes in the branching position in the latter two trees concern *S. orbiculus* (h) which branches at the base of the *Sorites* clade containing the specimens a–j.

4. Discussion

4.1. Peneroplidae are the ancestors of Soritidae

The general structure of the molecular trees (Figs. 1–3) is congruent with the classical, morphology-based phylogeny of Soritacea where Peneroplidae appear as the basal group (Hofker, 1953; Haynes, 1981). Our molecular data are confirmed by the fossil record, as the emergence of the first Peneroplidae predates by far the divergence of Soritidae, among which the earliest fossil archaiasines are reported from the Middle Eocene (Smout and Eames, 1958) and the earliest soritines from the Miocene (Haynes, 1981).

The monophyly of Peneroplidae in our molecular tree is unquestionable (100% bootstrap value), whereas the relationships between other Soritacea are less clear. High bootstrap support (96–100%) exists for the clade that groups archaisines and soritines together, but the associations within this clade are less resolved. In view of our molecular data, it seems accurate to divide the Soritacea in two families, Peneroplidae and Soritidae, and to further subdivide the Soritidae in two subfamilies, Archaiasinae and Soritinae, as already proposed by Gudmundsson (1994).

4.2. Laevipeneroplis is an archaiasine genus

Archaiasinae form a monophyletic cluster that also comprises *Laevipeneroplis* (Fig. 1). Although most authors recognize archaiasines as a separate taxon of family or subfamily rank (Seiglie et al., 1976; Loeblich and Tappan, 1988; Hallock and Peebles, 1993), the systematic position of *Laevipeneroplis* has remained controversial. Based on different external and internal morphological characters, *Laevipeneroplis* is placed by some authors among the Peneroplidae (Levy, 1977, Crapon de Caprona d'Ersu, 1983; Leutenegger, 1984; Hallock, 1999), whereas others (Seiglie et al., 1976) include it in the Archaiasinae. Gudmundsson (1994) splits the genus *Laevipeneroplis* because of some morphological differences (presence or absence of arciform growth mode and interior skeleton) and puts *L. proteus* at the base of the Archaiasinae, whereas *L. bradyi* is placed at the base of soritids.

Our molecular analyses indicate that all extant species of *Laevipeneroplis* are members of the subfamily Archaiasinae. The genus itself, however, is not well defined. The three species, that have been examined in this study branch separately from each other. One of them, *Laevipeneroplis* sp. that originates from the Western Pacific, appears as a sister

taxa to all Caribbean Archaiasinae (Figs. 1–3). Two other species, *Laevipeneroplis bradyi* and *Laevipeneroplis proteus*, are the respective sister taxa of the clades *Cyclorbiculina compressa* + *Broeckina* and *Archaias angulatus* + *Archaias lukasi* (Fig. 1), but their branching position within the Archaiasinae does not remain stable (Figs. 2 and 3). The basal position of *Laevipeneroplis* sp. is in agreement with morphological studies carried out by Seiglie et al. (1976) who proposed *L. proteus* or a close relative as an ancestor of the Archaiasinae.

The close connection between *Archaias angulatus* and *A. lucasi*, as suggested by our molecular data (Figs. 1–3) was already pointed out by Gudmundsson (1994), although the author groups both species together with *Cyclorbiculina compressa* because of some homologies concerning their internal and external test morphology. On the basis of the present molecular data, the relationships within the archaiasine subfamily cannot be fully resolved and further molecular studies are required to elucidate this problem.

The monophyly of Caribbean Archaiasinae is moderately well supported by our molecular data (Figs. 1–3). The presence of Pacific *Laevipeneroplis* sp. at the base of this clade (Figs. 1–3) would indicate that the origin of recent Archaiasinae lies in the Pacific or in the former Tethys region. Extant Archaiasinae are predominantely found in the Caribbean with the exception of *Laevipeneroplis* in the Pacific (Cheng and Zheng, 1978; Hallock and Peebles, 1993; Hallock, 1999) and Mediterranean (Leutenegger, 1984; Cimerman and Langer, 1991; Langer and Hottinger, 2000). Fossil archaiasines are known from the Tethys and the Pacific, as well as from the Caribbean region (Smout and Eames, 1958; Adams, 1976; Seiglie et al., 1976; Pringgoprawiro et al., 1998). It is possible that Archaiasinae originated in the Indo-Pacific and migrated later to the western Atlantic. The carbonate shelves and platforms of the Caribbean are generally distinguished by intermediate nutrient fluxes as a result of their proximity to continental runoff and coastal or topographic upwelling (Hallock, 1988a; Hallock et al., 1993). The proliferation of Archaiasinae in the Caribbean Sea might be explained by the presence of suitable environments, whereas the relative scarcity of appropriate ecological conditions in the Pacific might be a reason that recent archaiasine taxa failed to diversify in this region (Hallock, 1988a,b, 1999).

4.3. Parasorites appears as a sister taxa to the Soritinae

According to our molecular data (Figs. 1–3), the subfamily Soritinae forms a monophyletic group (bootstrap value of 60–70%), including *Parasorites* as a sister clade. Whereas the soritine genera *Sorites*, *Amphisorus* and *Marginopora* are distinguished by dinoflagellate symbionts, *Parasorites* possesses chlorophyte endosymbionts. The taxonomic position of the latter genus is highly controversial. Similar forms that are distinguished by cyclic growth and chambers divided by rudimentary partitions, exist in the Caribbean Sea as well as in the Pacific and were united by some authors under a single species (Hofker, 1952; Gudmundsson, 1994), whereas others stated that Carribean and Pacific forms belong to two different species (Levy, 1977; Crapon de Caprona d'Ersu, 1985).

Parasorites was first described by Seiglie et al. (1976), based on Caribbean material. Its type species is *Praesorites orbitolitoides*, which was originally described by Hofker (1930) from Pacific and Caribbean material. Caribbean forms that are akin to Hofker, 1930 *P. orbitolitoides* were included into the genus *Broeckina* by Levy (1977) and Crapon de Caprona d'Ersu (1985). According to Levy (1977) *Broeckina* only occurs in the Carribean Sea and is often confused with *P. orbitolitoides* (Hofker, 1930).

Similar forms from the Pacific were identified as *Parasorites orbitolitoides* by Hohenegger (1994) and Hohenegger et al. (1999), and described as *Sorites orbitolitoides* (type species: *P. orbitolitoides*, Hofker, 1930) by Lehmann (1961). Gudmundsson (1994) described similar forms from the Caribbean and the Pacific as *S. orbitolitoides* and regarded *Broeckina* and *Praesorites* as synonyms of the former species. Specimens of *Parasorites* examined in the present work correspond in their external features to *P. orbitolitoides* (Hohenegger 1994, Hohenegger et al., 1999) and *S. orbitolitoides* (Lehmann, 1961). The examined specimen of *Broeckina* corresponds in its external features to *Broeckina orbitolitoides* (Levy, 1977, Hallock and Peebles, 1993).

Our molecular data are in agreement with Levy

(1977) who considered *Parasorites* and *Broeckina* as two phylogenetically and geographically distinct genera. Our observations confirm that the tests of Caribbean *Broeckina* are delicate and more fragile than those of Pacific *Parasorites*, as mentioned by Levy (1977). Further external morphological differences between these two genera concern the arrangement and appearance of marginal apertures. In *Parasorites*, the marginal apertures are oval-shaped and arranged perpendicular to the apertural face (Plate 2, Fig. 2), whereas the marginal apertures of *Broeckina* are elongated and surrounded by a calcified rim. They are arranged parallel to the apertural face (Plate 3, 7). Moreover, some ecological differences exist between the two taxa: while living specimens of *Broeckina* are typically found on reef rubble in 15–30 m depth (Hallock and Peebles, 1993), *Parasorites* prefers sandy substrates and can be found up to 80 m depth (Hohenegger et al., 1999).

The taxonomic status of both genera needs to be revised. *Broeckina* was classified in the Soritinae by Munier-Chalmas (1882) and in the family Meandropsinidae by Levy (1977) and Crapon de Caprona d'Ersu (1985), but our genetical analyses clearly indicate that *Broeckina* is a member of the Archaiasinae. The phylogenetic position of *Parasorites* as inferred from molecular data suggests a basal relation with Soritinae (Figs. 1 and 2). This would be in agreement with Hofker (1953) who put *Praesorites orbitolitoides* at the base of the Soritinae. Hofker (1953) assumes that *P. orbitolitoides* developed from archaiasine ancestors, but its internal skeleton shows typical soritine charcteristics (Hofker, 1952). Molecular relationships between *Parasorites* and the Soritinae, however, are supported by relatively low bootstrap values (60–70%) and phylogenetic analysis of all chlorophyte endosymbionts from Archaiasinae and *Parasorites* reveals a single origin for the green algae (Pawlowski et al., 2001a,b). The taxonomic position of *Parasorites* stays thus a point of discussion.

4.4. Soritinae consist of two sister clades: Sorites/Marginopora vertebralis and Sorites/Amphisorus/M. cf. kudakajimaensis

Molecular data shed new light on the phylogeny of Soritinae. The general view of evolution within this group goes from simple forms (*Sorites*) to more complex (*Amphisorus*) to highly differentiated ones (*Marginopora*) (Lehmann, 1961). The increase of morphological complexity is illustrated by the development of a duplex skeleton (*Amphisorus*), doubling of annular canals and appearance of auxilliary chamberlets (*Marginopora*) (Lehmann, 1961; Gudmundsson, 1994). According to our results (Figs. 1–4), the genus *Amphisorus* is a sister group to *Sorites* and does not branch between *Sorites* and *Marginopora*, as would be expected if the evolution of Soritacea was driven by progressive morphological complexity. Moreover, it seems that the evolution of highly differentiated forms has taken place independently at least twice: *Marginopora vertebralis* and another form that was identified as *Marginopora* cf. *kudakajimaensis,* cluster separately, the first one as the sister group to the genus *Sorites*, the second one branches within the genus *Amphisorus* (Fig. 4).

Our results are supported by morphological studies. A comparison of three specimens of *Marginopora vertebralis* (d, e, f) and two specimens of *Marginopora* cf. *kudakajimaensis* (b, c), where half of the test was used for DNA extraction and the other half was investigated with the SEM, revealed that both species show some similarities with *Sorites* and *Amphisorus*, respectively (Plate 1, 1–4; Plate 2, 1–6). The apertures in *M. vertebralis* are rounded to circular with a calcified rim like in *Sorites*, while the apertures in *M.* cf. *kudakajimaensis* have an elongated to irregular shape as in *Amphisorus*. The chamber sutures in *Sorites* and *M. vertebralis* are wave-like, whereas they are slightly rounded in *Amphisorus* and in some *M.* cf. *kudakajimaensis* specimens. The investigated specimens of *M.* cf. *kudakajimaensis* show an internal median skeleton as it was described for *M. kudakajimaensis* (Gudmundsson, 1994). The internal skeleton, however, is only poorly developed in our forms. Because of their small size, it is difficult to decide whether our investigated specimens represent juvenile forms of *M. kudakajimaensis* or belong to a new, yet unknown species. Further molecular and morphological studies are necessary to clarify this question. A taxonomic revision, however, should be undertaken for the genus *Marginopora* as *M. vertebralis* clusters within another soritid genus.

More detailed morphological studies are needed to explain the presence of two genetically distinct groups

within the genus *Amphisorus* (Fig. 4). One group contains two soritid specimens that resemble in some external aspects *Amphisorus*, while the other comprises several specimens of *Amphisorus hemprichii* and *Marginopora* cf. *kudakajimaensis*. Morphological examination of the first group showed that *Sorites* sp._k and *Sorites* sp._l have thin tests and a delicate appearance, with a test diameter not exceeding 3 mm. A test fragment from *Sorites* sp._l was investigated with the SEM (Plate 1, 5 and 6). The specimen has elongated to irregular shaped apertures and slightly rounded chamber sutures, comparable to *Amphisorus* (Plate 1, 3 and 4). Similar specimens were described as *Sorites orbiculus* var. *marginalis* by Gudmundsson, 1994. From a molecular point of view, *Sorites* sp._k and *Sorites* sp._l may represent a different, ancestral lineage from which most of the recent *Amphisorus* species have evolved.

Morphological revision is needed in the case of *Sorites*, as it seems to be a paraphyletic group. Furthermore, two extant species of this genus, *Sorites orbiculus* and *Sorites marginalis* are not genetically separated and seem to be morphological variants of one species, an idea that was already proposed by Gudmundsson (1994). On the other hand, a *Sorites* specimen from Guam (*S. orbiculus*_h) branches at the basis of the whole *Sorites/Marginopora* clade (Fig. 4), indicating that morphologically similar forms of *S. orbiculus* might be divided in different genotypes. Interestingly, two specimens of *Sorites* collected in Caribbean Sea, *S. orbiculus*_c and *S. marginalis*_d mingle with Indo-Pacific representatives of this genus. This suggests that migration of large foraminifera between these two regions is possible, and more than a geographic barrier is needed to explain the isolation of Caribbean Archaiasinae.

4.5. Evolution of Soritacea is driven by endosymbiosis

Our data indicate that the acquisition and change in algal types as endosymbionts were crucial steps in the evolution of large miliolid foraminifera. The molecular division of Soritacea in three groups largely corresponds to their division based on different algal endosymbionts as proposed by Lee and Anderson (1991). The unique character of each symbiont transformation is confirmed by our molecular phylogenetic studies of soritid symbionts. Phylogenetic analysis of symbiont rDNA sequences reveals a single origin of all chlorophyte-symbionts found in Archaiasinae, including *Parasorites* (Pawlowski et al., 2001a,b). A similar study shows that the majority of *Symbiodinium*-like symbiotic dinoflagellates in Soritinae are specific to foraminiferans and do not mix with *Symbiodinium*-like symbionts of corals and other marine invertebrates (Pawlowski et al., 2001a,b).

Very little is known about the mechanisms of symbiont acquisition by foraminiferans. Our results indicate, that two factors play a certain role in the processus of divergence and radiation of a new group of symbiont-bearing foraminiferans. The first one is the necessity of morphological adaptation to a particular type of symbionts. For example, all members of the Soritinae are distinguished by discoidal tests with septula as internal partitions (Lehmann, 1961). Their flat tests with a large surface/volume area are optimized for sunlight capture and appear to be efficient in the uptake of nutrients that are diffusing from the underlying substratum (Hallock et al., 1991; Hallock and Peebles, 1993). Discoidal tests also evolved several times in Archaiasinae, but with a different internal skeleton (Seiglie et al., 1976; Gudmundsson, 1994). If soritine foraminiferans originate from Archaiasinae (Hofker, 1953; Haynes, 1981), then discoidal tests might have been passed on by the last common ancestor of Soritinae which could have had morphological characters similar to that of *Parasorites* (Hofker, 1953).

The radiation of larger foraminiferan lineages appears to be related to the ecological requirements of their symbionts (Hallock, 1999). Chlorophycean symbionts are known to be less effective in providing their hosts with nutrients than dinoflagellates (Hallock and Peebles, 1993). It is therefore not surprising that dinoflagellate-bearing Soritinae are abundant and diverse on oligotrophic Indo-Pacific coral reefs, but are not as common in the more mesotrophic waters of western Atlantic. Inversely, chlorophyte-bearing Archaiasinae radiated in the Caribbean Sea, while recent representatives of this group are uncommon in the Indo-Pacific (Debenay, 1985; Haig, 1988; Hallock and Peebles, 1993; Hohenegger, 1994; Hohenegger et al., 1999). As proposed by Hallock (1988a,b), the biogeographic patterns of distribution of the Soritacea appear to be related to the evolutionary history of

this group and its ability to adapt to particular ecological conditions.

Note added in proof

By courtesy of Dr. Gudmundsson, we received specimens of *M. Kudakajimaensis* and *S. orbiculus* var. *marginalis* that were originally from Prof. J.J. Lee. Specimens of the latter two species were sampled alive in summer 1987 in a lagoon environment on Kudakajima (Okinava, Japan), dried at room temperature and preserved on micropaleontological slides. The *M. kudakajimaensis* sample consisted of small specimens which, according to Dr. Gudmundsson, "presumably are young specimens of *M. kudakajimaensis*". DNA was extracted from half of the test of one specimen of *M. kudakajimaensis* and one specimen of *S. orbiculus* var. *marginalis*. Partial SSU rDNA was amplified by PCR, cloned and sequenced. Sequence analysis shows that *M. kudakajimaensis* branches with *M.* cf. *kudakajimaenisi*_a from Sesoko, while *S. orbiculus* var. *marginalis* branches with *S.=orbiculus*_h from Guam.

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References

Adams, G.C., 1976. Larger Foraminifera and the late Cenozoic history of the Mediterranean region. Paleogeogr. Paleoclimatol. Paleoecol. 20, 47–66.

Blainville, H.M.D., 1830. Mollusques vers et Zoophytes. Dictionnaire des Sciences Naturelles, vol. 60. F.G. Levrault, Paris.

Brady, H.B., 1884. Report on the Foraminifera dregded by H.M.S. Challenger, during the years 1873–1876. Report on the scientific results of the voyage of H.M.S. Challenger, Zoology IX, vol. 22. H.M. Stationers, London, pp. 1–814 Atlas, pls. 1-116.

Cahuzac, B., Poignant, A., 1997. Essai de biozonation de l'Oligo-Miocène dans les bassins europèens à l'aide des grands foraminifères néritiques. Bull. Soc. Géol. Fr. 168, 155–169.

Carpenter, W.B., 1861. Researches on Foraminifera — fourth and concluding series. Philos. Trans. R. Soc. London 150, 535–594.

Cheng, T.C., Zheng, S., 1978. The recent Foraminifera of the Xisha Islands Guangdong Province, China. Studia Marina Sinica 12, 148–310.

Cimerman, F., Langer, M.R., 1991. Mediterranean Foraminifera. Academia Scientiarum et. Artium Slovenica, Ljubljana, pp.118.

Crapon de Caprona d'Ersu, A., 1983. Contribution à l'étude des Soritidae actuels (Foraminifères)-2: sous-famille des Peneroplinae. Rev. Paléobiol. 2, 87–125.

Crapon de Caprona d'Ersu, A., 1985. Contribution à l'étude des Soritidae actuels (Foraminifères)-3: sous-familles des Archaiasinae, Meandropsininae et Soritinae et conclusions générales. Rev. Paléobiol. 4, 347–390.

Cushman, J.A., 1930. Foraminifera of the Atlantic Ocean. Bull. US Nat. Mus. 104, 1–79.

D'Orbigny, A.D., 1839. Foraminiféres. In: Ramon de la Sagra (Ed.), Histoire physique, politique et naturelle de l'Ile de Cuba, vol. 2, Zoologie. Paris, A. Bertrand: 224 pp.

De Vargas, C., Norris, R., Zaninetti, L., Gibb, W.S., Pawlowski, J., 1999. Molecular evidence of cryptic speciation in planktonic foraminifers and their relation to oceanic provinces. Proc. Natl. Acad. Sci. USA 96, 2864–2868.

Debenay, J.P., 1985. Recherches sur la sédimentation actuelle et les thanatocoenoses des Foraminifères de grande taille dans le lagoon sud-ouest et sur la marge insulaire sud de Nouvelle-Caledonie. Thesis, Univ. Aix-Marseille II, France, pp. 200.

Felsenstein, J., 1988. Phylogenies from molecular sequences: inference and reliability. Annu. Rev. Genet. 22, 521–565.

Fichtel, L. and Moll, J.P.C., 1798. Testacea microscopica, aliaque minuta ex generibus Argonauta et Nautilus, ad naturam picta et descripta. Vindobona, Camesina.

Forskal, P., 1775. Descriptiones Animalium. Hauniae. Carsten Niebuhr, Copenhagen.

Galtier, N., Gouy, M., 1996. SEAVIEW and PHYLO_WIN: two graphic tools for sequence alignment and molecular phylogeny. Comput. Appl. Biosci. 12, 543–548.

Gudmundsson, G., 1994. Phylogeny, ontogeny and systematics of Recent Soritacea Ehrenberg 1839 (Foraminiferida). Micropaleontology 40, 101–155.

Haig, W.D., 1988. Miliolid Foraminifera from inner neritic sand and mud facies of the Papuan Lagoon, New Guinea. J. Foraminiferal Res. 18, 203–236.

Hallock, P., 1988a. Diversification in algal symbiont-bearing Foraminifera: a response to oligotrophy? Revue de Paleobiologie 2 (Benthos '86), 789–797.

Hallock, P., 1988. Interoceanic differences in Foraminifera with symbiotic algae: a result of nutrient supplies? Proceedings of

the Sixth International Coral Reef Symposium, Townsville, Australia, 8–12 August 1988, 3: 251–255.

Hallock, P., Peebles, W.M., 1993. Foraminifera with chlorophyte endosymbionts: habitats of six species in the Florida Keys. Mar. Micropaleontol. 20, 277–292.

Hallock, P., Röttger, R., Wetmore, K., 1991. Hypotheses on form and function in Foraminifera. In: Lee, J.J., Anderson, O.R. (Eds.), Biology of the Foraminifera. Academic Press, New York, pp. 41–72.

Hallock, P., Müller-Karger, F.E., Halas, J.C., 1993. Coral Reef Decline — Anthropogenic Nutrients and the Degradation of Western Atlantic and Caribbean Coral Reefs. Res. Explor. 9 (3), 358–378.

Hallock, P., 1999. Symbiont-bearing Foraminifera. In: Sen Gupta, K.B. (Ed.), Modern Foraminifera. Kluwer Academic Publishers, Dordrecht, pp. 123–140.

Hatta, A., Ujiie, H., 1992. Benthic Foraminifera from the Coral Seas between Ishigaki and Iriomote Islands, Southern Ryukyu Island Arc, Northwest Pacific. Part 1. Systematic descriptions of Textulariina and Miliolina. Bull. Coll. Scie. Univ. Ryukyus 53, 49–119.

Haynes, J.R., 1981. Foraminifera. Wiley, New York.

Hillis, D.M., Bull, J.J., 1993. An empirical test of bootstrapping as amethod for assessing confidence in phylogenetic analysis. Syst. Biol. 42, 182–192.

Hofker, J., 1930. The Foraminifera of the Siboga expedition, part II. Siboga-Expeditie Monografen. No. 4a. E. J. Brill, Leiden.

Hofker, J., 1950. Recent Peneroplidae Part I. J. R. Microscop. Soc. London 70, 388–396.

Hofker, J., 1951. Recent Peneroplidae, Part III. Genus Puteolina nov. gen. (including the former genus Archaias). J. R. Microscop. Soc. London 71, 450–463.

Hofker, J., 1952. Recent Peneroplidae Part IV. Genus Orbitolites. J. R. Microscop. Soc. London 72, 102–122.

Hofker, J., 1953. Recent Peneroplidae Part V. Reproduction of the Peneroplidae. J. R. Microscop. Soc. London 73, 40–46.

Hohenegger, J., 1994. Distribution of living larger Foraminifera NW of Sesoko-Jima Okinawa, Japan. Mar. Ecol. 15, 291–334.

Hohenegger, J., Yordanova, E., Nakano, N., Tatzreiter, F., 1999. Habitats of larger Foraminifera on the upper reef slope of Sesoko Island, Okinawa, Japan. Mar. Micropaleontol. 36, 109–168.

Holzmann, M., Pawlowski, P., 1996. Preservation of Foraminifera for DNA extraction and PCR Amplification. J. Foraminiferal Res. 26, 264–267.

Hottinger, L., 1983. Reconstruction of Marine Paleoenvironments. In: Meulenkamp, J.E. (Ed.), Processes determining the distribution of larger Foraminifera in space and time. Utrecht Micropaleontol. Bull. 30, 239–253.

Kimura, M., 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. J. Mol. Evol. 16, 111–120.

Lamarck, J.B., 1816. Histoire naturelle des animaux sans vertébres. Histoire naturelle des animaux sans vertébres, vol. 2. Verdiére, Paris.

Langer, M.R., Hottinger, L., 2000. Biogeography of selected 'larger' Foraminifera. Micropaleontology 46 (suppl. 1), 105–126.

Larsen, N., Olsen, G.J., Maidak, B.L., McCaughey, M.J., Overbeek, R., Macke, T.J., Marsh, T.L., Woese, C.R., 1993. The ribosomal database project. Nucl. Acids Res. 21, 3021–3023.

Lee, J.J., Hallock, P., 1987. Algal symbiosis as a driving force in the evolution of larger Foraminifera. Ann. New York Acad. Sci. 503, 330–347.

Lee, J.J., 1990. Fine structure of the rhodophycean Porphyridium purpureum in situ in Peneroplis pertusus (Forskal) and *P. acicularis* (Batsch) and in axenic culture. J. Foraminiferal Res. 20, 162–169.

Lee, J.J., Anderson, O.R., 1991. Symbiosis in Foraminifera. In: Lee, J.J., Anderson, O.R. (Eds.), Biology of Foraminifera. Academic Press, London.

Lehmann, R., 1961. Strukturanalyse einiger Gattungen der Subfamilie Orbitolitinae. Ecol. Geol. Helv. 54, 597–667.

Leutenegger, S., 1984. Symbiosis in benthic foraminifera: specificity and host adaptation. J. Foraminiferal Res. 14, 16–35.

Levy, A., 1977. Révision micropléontologique des Soritidae actuels Bahamiens, Un nouveau genre: Androsina. Bull. Cent. Rech. Explor.-Prod. Elf-Aquitaine 1, 393–449.

Lockhart, P.J., Steel, M.A., Hendy, M.D., Penny, D., 1994. Recovering evolutionary trees under a more realistic model of sequence evolution. Mol. Biol. Evol. 2, 605–612.

Loeblich, A.J.R., Tappan, H., 1964. Sarcodina chiefly "The camoebians " and Foraminiferida. In: Moore, R.C. (Ed.), Treatise on Invertebrate Paleontology, part C, 1–2. Geological Society of America and University of Kansas Press, Lawrence, p. 900.

Loeblich, A.J.R., Tappan, H., 1988. Foraminiferal Genera and their Classification, vol. 1–2. Van Nostrand Reinhold, New York.

McEnery, M., Lee, J.J., 1981. Cytological and fine structural studies of three species of symbiont-bearing larger Foraminifera from the Red Sea. Micropaleontology 27, 71–83.

Munier-Chalmas, E., 1882. Un genre nouveau de foraminifères sénoniens. Bull. Soc. Géol. France, sér. 3 10, 471–472.

Neefs, J.M., Van der Peer, Y., De Rijk, P., Chapelle, S., De Wachter, R., 1993. Compilation of small ribosomal subunit RNA structures. Nucl. Acids Res. 21, 3025–3049.

Olsen, G.J., Matsuda, H., Hagstrom, R., Overbeek, R., 1994. Fast DNAml: A tool for construction of phylogenetic trees of DNA sequences using maximum likelihood. Comput. Appl. Biosci. 10, 41–48.

Pawlowski, J., Bolivar, I., Fahrni, J.F., de Vargas, C., Bowser, S., 1999. Molecular evidence that Reticulomyxa filosa is a freshwater naked foraminifer. J. Eukaryot. Microbiol. 46, 612–617.

Pawlowski, J., 2000. Introduction to the molecular systematics of foraminifera. Micropaleontology 46 (suppl. 1), 1–112.

Pawlowski, J., Holzmann, M., Fahrni, J., Hallock, E., 2001a. Molecular identification of algal endosymbionts in large miliolid foraminifers 1 chlorophytes. J. Eukaryot. Microbiol. 48, 362–367.

Pawlowski, J., Holzmann, M., Fahrni, J., Pochon, X., Lee, J.J., 2001b. Molecular identification of algal endosymbionts in large miliolid foraminifers: 2 Dinoflagellates. J. Eukaryot. Microbiol. 48, 368–373.

Pringgoprawiro, H., Kadar, D., Skwarko, K.S., 1998. Foraminifera in Indonesian stratigraphy. Cenozoic Benthonic Foraminifera 2, 121–141.

Reichel, M., 1937. Etudes sur les Alvéolines. Mém. Soc. Paléontol. Suisse 59, 95–147.

Saitou, N., Nei, M., 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. Mol. Biol. Evol. 4, 406–425.

Seiglie, A.G., Grove, K., Rivera, A.J., 1976. Revision of some Caribbean Archaiasinae, new genera, species and subspecies. Ecol. Geol. Helv. 70, 855–883.

Smout, H.A., Eames, E.F., 1958. The genus Archaias (Foraminifera) and its stratigraphic distribution. Paleontology 1, 207–225.

Swofford, D. L., 2000. PAUP* Phylogenetic Analysis using parsimony (* and other methods). Version 4. Sinauer Assoc., Sunderland, MA.